habitats release eggs and sperm into the water column, and fertilization takes place between free-floating gametes. This mode of sexual reproduction is exhibited by many extant marine invertebrates and could plausibly have been used by ancestral metazoans. The evolution of cytostatic arrest could have allowed oocytes to be produced and released independently of fertilization, without running the risk of premature parthenogenetic cleavage.

Several outstanding questions remain when considering the evolution of gametogenesis and the roles of *mos* genes in this process: why were multiple copies of *mos* retained in cnidarians, while bilaterians kept only one? Does the absence of *mos* in the sponge genome correspond with a lack of cytostatic arrest in sponge oocytes? Similarly, do eukaryotic protists undergo parasexual cleavages without any arrest phases, in accordance with the absence of *mos* homologues? Are choanoflagellates, lacking *mos*, capable of any kind of reduction division? While answers to these questions will undoubtedly require many more years to achieve, we can now begin to speculate as to the relative evolutionary histories of the many roles of *c-mos*: the meiotic maturation function shared by *Clytia* and deuterostomes suggest that the secondary arrest role of *c-mos* is an ancient one, while its primary arrest role may be more recently evolved.

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Olfaction: Chemical Signposts along the Silk Road

A recent study on the reception of olfactory cues by silkworm larvae illustrates how the convergence of genomic, physiological and ecological data promises to shed light on the origins and evolution of chemically mediated interactions between plants and insects.

Mark C. Mescher[1] and Consuelo M. De Moraes[2]

For insects, olfaction is the primary sensory modality used to acquire information about the world [1]. Information obtained from the detection of odor cues helps insects to negotiate complex environments, locate valuable resources, and avoid toxic or otherwise life-threatening conditions. Among the most important of these cues are pheromones emitted by conspecific individuals, which convey socially relevant information — for example, by signaling the presence of potential mates. But insects also detect and respond to other ambient odors that can provide valuable information about local conditions. Foremost in significance among these 'general odorants' are volatile compounds emitted by plants. Plants dominate the biomass of terrestrial ecosystems and engage in continuous gas exchange with the surrounding atmosphere, creating a rich olfactory landscape for other organisms. Moreover, the composition of the volatile blend released by plants differs among species and also varies systematically in response to a wide array of environmental conditions, including insect feeding and pathogen infection [2]. As a result, volatile cues can potentially provide foraging insects

Figure 1. A fifth-instar silkworm caterpillar feeding on mulberry leaves (photo by Naoko Yoshinaga).

with a great deal of information about the identity and status of emitting plants [3–6].

In deciphering this information, insects may rely on the detection of specific compounds characteristic of a particular plant taxon — or diagnostic of, say, feeding damage caused by a particular herbivore species. Alternatively, they may detect volatile compounds that are more widely distributed among plant species, and attempt to recognize characteristic patterns in the relative ratios of constituent compounds [7]. The latter strategy might seem difficult to implement, as foraging insects constantly encounter a diverse array of ambient odors, including potentially hundreds of different plant-derived compounds, but volatile blends emitted by a point source appear to be somewhat robust when sampled at sufficiently small spatial scales — as the mass movement of air occurs at rates that tend to overwhelm the diffusion individual blend components — and there is evidence that the co-location of functional groups of olfactory receptor neurons within individual sensilla of the insect antenna provides fine-scale spatio-temporal resolution [8–10].

Some insects have indeed been shown to respond specifically to volatile compounds diagnostic of particular plant species [7,11]. Several crucifer specialists, for example, have olfactory receptor neurons finely tuned for the detection of isothiocyanates, volatile catabolites of the glucosinolate compounds that characterize these plants [9,12]. But in a far greater number of systems, host finding appears to involve mixtures of more common volatile compounds [7,13], with specificity determined by the evaluation of specific ratios among components [14]. Thus, the current weight of evidence suggests that most insects detect a wide range of plant-derived volatile compounds and respond to information obtained from the recognition of characteristic patterns in the composition of the blend [7,11].

A new study by Tanaka *et al.* [15], however, indicates that the movement of silkworm larvae (*Bombyx mori*) toward the mulberry leaves on which they feed (Figure 1) is guided by a single compound, *cis*-jasmone, detected by a highly tuned receptor. Several additional compounds that had previously been implicated in host location by *B. mori* were found to be only weakly attractive, even at concentrations far exceeding those normally encountered, while *cis*-jasmone presented in isolation induced a robust, dose-dependent behavioral response equivalent to that of the overall blend. Functional analyses conducted by expressing 20 putative larval olfactory receptor genes in *Xenopus* oocytes identified a single receptor, BmOr-56, that responds strongly to *cis*-jasmone; and subsequent experiments showed that the ability of compounds structurally similar to *cis*-jasmone to elicit a response from BmOr-56 was predictive of their ability to attract *B. mori* larvae.

That the attraction of silkworm larvae to mulberry leaves appears to be governed by a single finely tuned receptor similar to many insect-pheromone systems is intriguing, but the broader implications of this finding for understanding the evolution of insect olfactory perception and response are currently difficult to divine. While *cis*-jasmone has previously been reported to be a plant volatile associated with insect damage [16,17], its emission from undamaged leaves has not been reported for plant species other than mulberry; hence, *cis*-jasmone may be a reliable cue for *B. mori* larvae. More generally, it is possible that the complexity of volatile cues exploited by lepidopteran larvae diverges from that of cues exploited by adults, which forage for host plants over much larger areas. While the olfactory responses of caterpillars to volatile cues are not well documented, several previous studies have reported larval responses to individual host plant compounds [18].

Another factor potentially contributing to the simplicity of the olfactory response observed in *B. mori* is the long history of silkworm cultivation by humans. It is typical for sericulturists to have female moths oviposit on paper and then allow the larvae to migrate to the mulberry leaves on which they feed. In this context, it is likely that *cis*-jasmone provides a sufficient and reliable cue to the location of food, and the simplicity of the larval olfactory response may reflect the highly predictable environments in which these domesticated larvae develop. It is clearly to be expected that the reception and processing of chemical cues will evolve to match key aspects of an insect's ecology and social environment [1]. For example, it has previously been suggested that the greatly reduced repertoire of gustatory receptors exhibited by honeybees reflects the mutualistic relationship between bees and their food plants — because the nectar on which bees feed typically lacks defensive compounds, such as alkaloids, that plants deploy against

leaf-feeding herbivores, bees may have little need for the bitter taste receptors that other phytophagous insects use to detect these compounds [19].

While sericulture is not as ancient as the relationship between bees and flowers, silkworms were being cultured in China by 2500 B.C. and probably much earlier. The potential for evolutionary change over this period is amply demonstrated by the adults of *B. mori*, which have lost the ability to fly and do not feed. Moreover, while adult *B. mori* express BmOr-56 they do not respond to *cis*-jasmone or, apparently, to any odor cues apart from the sex pheromone, bombykol, which still guides reproduction. But, though an intriguing possibility, it is currently impossible to say whether the simplicity of the observed response of domesticated *B. mori* larve to olfactory cues from their host plant reflects the reduction of a more complex suite of responses employed by the free-living ancestors. To answer this question, it would be very useful to investigate the olfaction and behavior of adults and larvae of *B. mandarina,* the nearest wild relative of *B. mori.*

What is clear from the new study [15], however, is the power of the approach employed here to reveal patterns of olfactory reception and response that bear directly on such questions by integrating genomic, ecological, and physiological data. The convergence of these empirical approaches promises to provide new insights into the ecological significance of volatile-mediated interactions among plants and insects, and into their evolutionary origins, which are currently little known. To that end, exploration of differences between natural and human-dominated (for example, agricultural) systems, as suggested above for *B. mori*, may be a valuable starting point for future work. A surprising aspect of much past work in plant–insect chemical ecology is the frequent documentation of complex and sophisticated interactions — mediated by plant volatiles — occurring in agricultural assemblages of plant and insect species that do not reflect natural associations. It is often not clear whether such apparent adaptation reflects rapid evolution of insect olfactory responses in these systems, inherent flexibility in insects' detection and response systems, or the retention of adaptive mechanisms evolved in ancestral environments. A comparative approach employing the analytical tools discussed here may soon answer such questions, while perhaps also teaching us how to manipulate such interactions to enhance the sustainable management of agricultural ecosystems.

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Visual Perception: Saccadic Omission — Suppression or Temporal Masking?

Although we don't perceive visual stimuli during saccadic eye movements, new evidence shows that our brains do process these stimuli and they can influence our subsequent visual perception.

Michael R. Ibbotson and Shaun L. Cloherty

People shift their gaze between objects of interest using rapid pre-planned eye movements known as saccades. While saccades are essential for pointing the eye at targets in the scene, they induce rapid and potentially disturbing visual motion across the retina. Yet in everyday experience these rapid scene shifts are not perceived. In fact, most visual stimuli presented just